Sex Differences and Allee Effects Shape the Dynamics of Sex-Structured Invasions

Allison K. Shaw*[a], Hanna Kokko[b] and Michael G. Neubert[c]

[a]Department of Ecology, Evolution, and Behavior, University of Minnesota, MN 55108 USA
[b]Department of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland
[c]Biology Department, MS 34, Woods Hole Oceanographic Institution, Woods Hole, MA 02543 USA

*Corresponding author: ashaw@umn.edu

Running headline: Sex-structured invasion dynamics

This is the peer reviewed version of the following article:
Shaw AK, Kokko H, Neubert MG (2017) "Sex differences and Allee Effects shape the dynamics of sex-structured invasions" *Journal of Animal Ecology*.
which has been published in final form at http://onlinelibrary.wiley.com/doi/10.1111/1365-2656.12658/full. This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Self-Archiving.

Summary

1. The rate at which a population grows and spreads can depend on individual behaviour and interactions with others. In many species with two sexes, males and females differ in key life history traits (e.g. growth, survival, dispersal), which can scale up to affect population rates of growth and spread. In sexually reproducing species, the mechanics of locating mates and reproducing successfully introduce further complications for predicting the invasion speed (spread rate), as both can change nonlinearly with density.

2. Most models of population spread are based on one sex, or include limited aspects of sex differences. Here we ask whether and how the dynamics of finding mates interact with sex-specific life history traits to influence the rate of population spread.

3. We present a hybrid approach for modelling invasions of populations with two sexes that links individual-level mating behaviour (in an individual-based model) to population-level dynamics (in an integrodifference equation model).

4. We find that limiting the amount of time during which individuals can search for mates causes a demographic Allee effect which can slow, delay or even prevent an invasion. Furthermore, any sex-based asymmetries in life history or behaviour (skewed sex ratio, sex-biased dispersal, sex-specific mating behaviours) amplify these effects. In contrast, allowing individuals to mate more than once ameliorates these effects, enabling polygynandrous populations to invade under conditions where monogamously mating populations

would fail to establish.

5. We show that details of individuals' mating behaviour can impact the rate of population spread. Based on our results, we propose a stricter definition of a mate-finding Allee effect, which is not met by the commonly used minimum mating function. Our modelling approach, which links individual- and population-level dynamics in a single model, may be useful for exploring other aspects of individual behaviour that are thought to impact the rate of population spread.

Keywords

integrodifference equations, invasion speed, mate-finding Allee effect, mating functions, sex-biased dispersal, spatial spread

Introduction

The key characteristics of a potential invasion are whether a population will be able to establish and, if it does, how fast it will subsequently grow and spread. Often there is a threshold size or density below which a population will be unable to successfully establish (Volterra, 1938; Tobin *et al.*, 2007). Early theoretical work predicted that, when populations do establish, they should spread at a constant rate, assuming identical individuals move diffusely in a homogeneous environment (Skellam, 1951). More recent theory has explored how invasion speed can be influenced by a variety of factors, including long-distance dispersal (Kot, Lewis & van den Driessche, 1996), population structure (Neubert & Caswell, 2000), demo-

graphic stochasticity (Kot *et al.*, 2004), spatial heterogeneity (Li, Fagan & Meyer, 2015), environmental stochasticity (Lewis & Pacala, 2000), temporal variability (Neubert, Kot & Lewis, 2000; Caswell, Neubert & Hunter, 2011; Schreiber & Ryan, 2011), and evolution (Kanarek & Webb, 2010; Phillips, Brown & Shine, 2010; Perkins *et al.*, 2013). However, the majority of these invasion models assume an asexual population and may fail to capture dynamics of spatial spread in sexually reproducing species for two reasons.

First, individuals in sexually reproducing species must locate at least one mate in order to reproduce successfully. These species may experience a mate-finding Allee effect where an individual's probability of finding mates decreases with lower population density (Dennis, 1989; Wells *et al.*, 1998). This so-called "component Allee effect" (which impacts one 'component' of an individual's fitness) results in a demographic Allee effect if, over some range of density, the overall population growth rate increases with a (small) increase in population density (Stephens, Sutherland & Freckleton, 1999). Since Allee effects tend to have the strongest impact at low population sizes and densities, they are especially likely to affect the viability of endangered species, whose numbers have been reduced (Courchamp, Berec & Gascoigne, 2008), and the ability of invasive species to establish and spread from an initially low density at newly established sites (Keitt, Lewis & Holt, 2001; Taylor & Hastings, 2005).

Second, in many cases, males and females differ in key life history traits. Sex differences can occur in age of sexual maturity, reproductive period length and total lifespan (Short & Balaban, 1994; Fairbairn, 2013) Males and females can also differ in their tendency to disperse, and total dispersal distance travelled (Greenwood, 1980; Clarke, Sæther & Røskaft, 1997; Miller *et al.*, 2011). Since

the speed of an invasion depends on both demographic and dispersal parameters (Skellam, 1951; Neubert & Caswell, 2000), sex-specific differences in any of these parameters can potentially alter the rate of spread. While the consequences of Allee effects for spatial spread has been studied (Fife & McLeod, 1977; Lewis & Van Den Driessche, 1993; Kot, Lewis & van den Driessche, 1996; South & Kenward, 2001; Taylor & Hastings, 2005; Jerde, Bampfylde & Lewis, 2009), this is rarely done while simultaneously taking into account sex differences in dispersal.

To overcome these limitations, we take advantage of two approaches already developed, that allow us to study spatial spread in sex-structured populations. Miller *et al.* (2011) developed an integrodifference equation model that tracks male and female density separately, allowing the exploration of how sex differences in dispersal and the nature of the mating system jointly influence the spread rate. Although this is a (relatively) mathematically tractable approach, it ignores non-linearities in mating (introduced by mate-finding difficulties) at low density. Shaw & Kokko (2014, 2015) developed an individual-based simulation model with male and female individuals, allowing them to include a mechanistic mate-finding Allee effect by explicitly modelling the mate finding process. Although this approach allows for inclusion of more biological detail than the approach of Miller *et al.* (2011), it is less mathematically tractable and requires extensive simulation time. These two approaches have each demonstrated that sex-specific dynamics (sex-biased dispersal, mate finding) can dramatically influence a population's spread rate.

Here we present a hybrid approach that couples individual-based simulation and integrodifference equation modelling methods. We model mating dynamics using individual-based simulations from Shaw & Kokko (2014) and then insert

these into the integrodifference equation framework from Miller *et al.* (2011) to describe the growth and spatial spread of a population. We compare our results using the simulated mating dynamics to results using two different mathematical approximations of the mating dynamics. We show that sex-specific mating behaviour and sex differences in life history each affect the population growth rate, probability of establishment, and dynamics of spread, and furthermore that mating and life history effects are interactive. We expect that this hybrid framework will be a useful tool for future studies that aim to explore how other aspects of individual behaviour influence population outcomes, particularly in a spreading context.

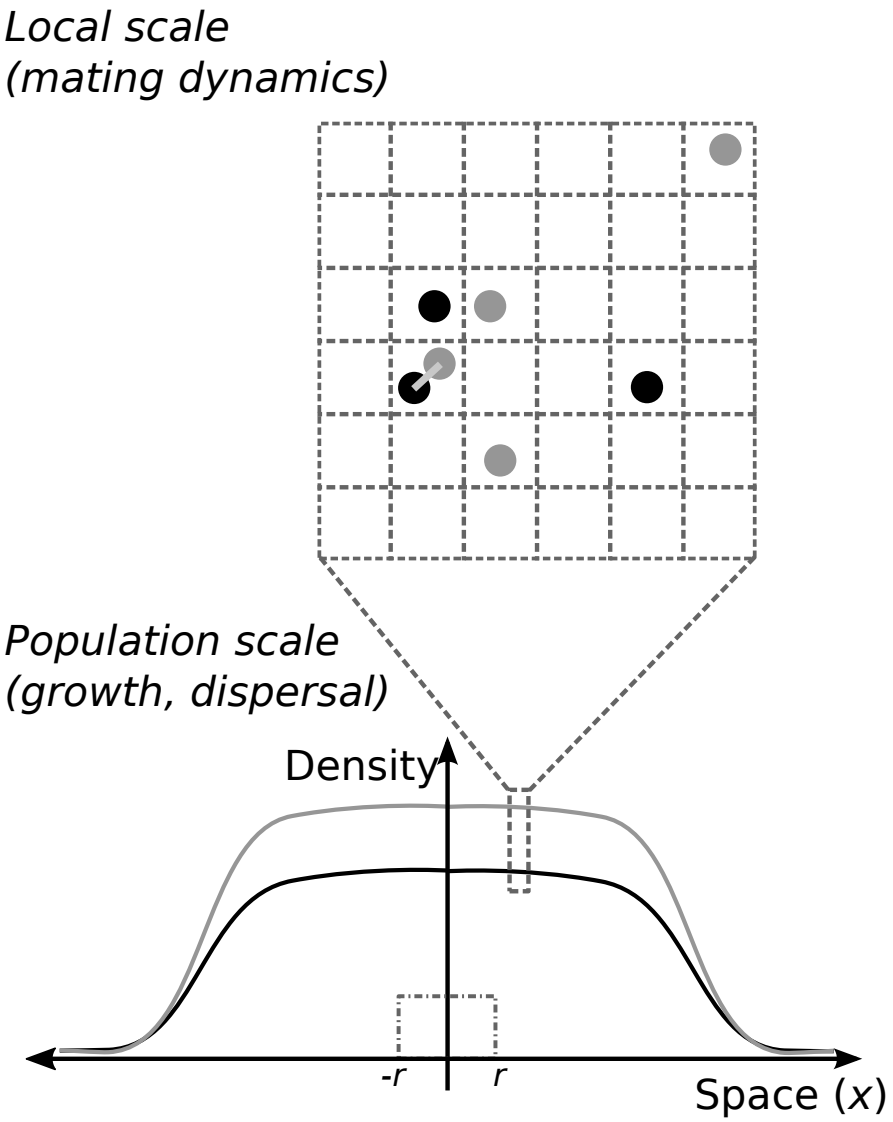
Materials and methods

Full model code is available from Dryad (Shaw, Kokko & Neubert, 2016).

Mating dynamics

We start by describing the mating dynamics that occur locally among f females and m males (Fig. 1). Let $\mathfrak{B}(f, m)$ be the total number of matings that occur at a location, i.e. the mating function. We first consider a mating function derived explicitly from individual-based simulations of the mate finding and mating process. Then we consider two functions that are approximations of the mating process: the mass action function and the Hölder mating function. As we show below, as special cases these also produce simpler formulations such as the minimum mating function (Bessa-Gomes, Legendre & Clobert, 2010) where the number of matings simply equals the number of individuals of the rarer sex.

Figure 1: Schematic showing the two scales of our hybrid model. Mating occurs between f females (black) and m males (grey) at a local scale. A male and female in the same patch can pair (indicated by a line) and mate. (Note that each patch may contain more than one male and/or female.) The density of males and females is tracked at the population scale (here shown as the density of individuals immediately after births occur). The dashed-dotted line shows the initial population density distribution for each simulation.



Individual-based functions

The first mating function is based on the individual-based simulation developed by Shaw & Kokko (2014, 2015). We determine the number of monogamous mating pairs that form from f females and m males as follows (we address the case of non-monogamy later). We first randomly distributed f females and m males in patches across a 10-by-10 square lattice with wrapping boundaries. Within each time step ($t = 1, \ldots, \tau$) that follows, each individual can make one mate search decision, then form pairs (if possible). Once individuals are part of a pair, they do not search in subsequent time steps. This searching-pairing process is repeated for τ time steps, after which the total number of formed pairs is recorded. Note that each patch can contain any number of males and females (up to m and f, respectively).

In this part of the model, each individual's movement is governed by a mate search function. During the mate search decision, each individual chooses to stay in their patch with a probability that we model using a logistic function of the number of females and males present,

$$p_{\mathrm{f}} = \frac{1}{1 + 0.5e^{-a(R_{\mathrm{FS}} - f_i)} + 0.5e^{a(R_{\mathrm{FO}} - m_i)}} \tag{1a}$$

$$p_{\mathrm{m}} = \frac{1}{1 + 0.5e^{a(R_{\mathrm{MO}} - f_i)} + 0.5e^{-a(R_{\mathrm{MS}} - m_i)}} \tag{1b}$$

for females and males respectively. Individuals choose to leave their patch with probability $1 - p_{\mathrm{f}}$ and $1 - p_{\mathrm{m}}$. Here, f_i and m_i are the number of unpaired females and males in the ith patch, R_{FS} and R_{FO} are fixed strategy parameters for a

female's response to individuals of the same and opposite sex, R_{MS} and R_{MO} are fixed strategy parameters for a male's response to individuals of the same and opposite sex, and a is the shape parameter of the strategy as described in Shaw & Kokko (2014). For $a > 0$ (the only case we consider) a female is more likely to stay in a patch that has few females and many males, and a male is more likely to stay in a patch that has many females and few males.

To minimize confusion later on, we refer to movement that occurs during this mating process as 'searching' to distinguish it from the 'dispersal' movement that we include in the full population model below. Here, we consider three scenarios, distinguished by the values of the search strategy parameters: unbiased searching (both males and females search for mates; $R_{\mathrm{FS}} = R_{\mathrm{FO}} = R_{\mathrm{MS}} = R_{\mathrm{MO}} = 1$), male-biased searching (only males search and females are stationary; $R_{\mathrm{FS}} \to \infty$, $R_{\mathrm{FO}} \to -\infty$, $R_{\mathrm{MS}} = R_{\mathrm{MO}} = 1$), and female-biased (only females search and males are stationary; $R_{\mathrm{FS}} = R_{\mathrm{FO}} = 1$, $R_{\mathrm{MS}} \to -\infty$, $R_{\mathrm{MO}} \to \infty$). The parameter values $R_{\mathrm{jS}} = R_{\mathrm{jO}} = 1$ indicate that an individual of sex j has a 50% probability of leaving a patch with one member of the same sex and one member of the opposite sex, will be more likely to leave patches with more members of the same sex, and less likely to leave patches with more members of the opposite sex. (See Shaw & Kokko (2014, 2015) for graphical examples of these probability functions.)

Individuals search serially, in random order within each time step t. If an individual chooses to leave its patch, it moves randomly to one of the four patches adjacent to its current patch (with wrapping boundaries across the lattice). After all individuals have made a mate search decision, pairs form. In each patch i that contains both females and males, $\min(f_i, m_i)$ pairs are formed. Note that once individuals are paired, they are ignored by non-paired individuals; mate search

decisions are only made based on the densities of unpaired males and females.

For comparison, we also ran simulations allowing for multiple matings (polygynandry). In these simulations, both males and females searched for mates ($R_{\mathrm{FS}} = R_{\mathrm{FO}} = R_{\mathrm{MS}} = R_{\mathrm{MO}} = 1$). Here, all mating pairs are temporary, and new pairs can potentially form at every time step. All individuals (whether or not they mated in the past) make a mate search decision at every time step, according to equation (1) which (for this set of simulations) depended on the total number of males and females in the current patch (regardless of mating history). At the end of these simulations, instead of calculating the number of pairs that formed, we counted the number of females who had mated at least once.

We ran a total of $1,764,000$ simulations. For each of the four scenarios (unbiased, male-biased, female-biased, polygynandrous matings), we ran simulations with all factorial combinations of $f = 1, 11, 21, ..., 191, 200$ females and $m = 1, 11, 21, ..., 191, 200$ males for $\tau = 1, 2, 3, ..., 500$ time steps, to generate four corresponding mating functions ($\mathfrak{B}_{\mathrm{u}}$, $\mathfrak{B}_{\mathrm{m}}$, $\mathfrak{B}_{\mathrm{f}}$ and $\mathfrak{B}_{\mathrm{p}}$) as a function of the number of females (f), number of males (m), and mate search time (τ). We ran $1,000$ replicates for each combination of parameters and then averaged across replicates.

Mass action function

Next, we consider a second mating function that is an approximation of the pair formation process. This approach is similar to the one used by Veit & Lewis (1996). The change in the number of females, males and pairs as a function of search time

can be described by the set of equations

$$\frac{df}{d\hat{\tau}} = -M(f,m) \tag{2a}$$
$$\frac{dm}{d\hat{\tau}} = -M(f,m) \tag{2b}$$
$$\frac{dp}{d\hat{\tau}} = M(f,m) \tag{2c}$$

where $M(f,m)$ is the rate of pair formation and $0 \leq \hat{\tau} \leq \tau$. By assuming random searching of males and females, we can model the pair formation process with the law of mass action

$$M(f,m) = cfm = c(f_0 - p)(m_0 - p) \tag{3}$$

where f_0 and m_0 are the initial number of males and females present. After a fixed length of time τ, the number of pairs that formed is equal to

$$\mathfrak{B}_{\mathrm{a}} = \begin{cases} \frac{f_0 m_0 \{1 - \exp[(m_0 - f_0)c\tau]\}}{f_0 - m_0 \exp[(m_0 - f_0)c\tau]} & \text{if } f_0 \neq m_0 \\ \frac{n_0^2}{n_0 + (1/c\tau)} & \text{if } f_0 = m_0 = n_0 \end{cases} . \tag{4}$$

As $\tau \to \infty$, all possible pairs form and $\mathfrak{B}_{\mathrm{a}}(\tau) = \min(f_0, m_0)$, i.e., the minimum mating function. Similar to the individual-based mating function above, we calculated the number of matings for each $f = 1, 11, 21, ..., 191, 200$ females and $m = 1, 11, 21, ..., 191, 200$ males for $\tau = 1, 2, 3, ..., 500$ time steps with $c = 0.01$ ($c\tau = 0.01, 0.02, 0.03, ..., 5$). The end result is the mating function $\mathfrak{B}_{\mathrm{a}}$ as a function of the number of females (f), number of males (m), and $c\tau$.

Hölder mean function

Finally, we consider an approximation for the number of matings without the pair formation dynamics. Here, the mating function is given by

$$\mathfrak{B}_{\mathrm{h}}(f_t, m_t) = [\beta f_t^{\alpha} + (1-\beta) m_t^{\alpha}]^{1/\alpha} \tag{5}$$

with shape parameter $\alpha < 0$ and weight parameter $0 \leq \beta \leq 1$, which describes the relative weighting of females and males. This is a family of weighted means (Hölder means), first suggested to describe mating dynamics by Hadeler (1989), and commonly used as a mating function (including by Miller *et al.* 2011). For different values of the shape parameter α and the weight parameter β this function encompasses a number of commonly used mating functions. For $\alpha = -\infty$ and $\beta = 0.5$ (the minimum mating function) we recover the mass action mating function (eqn. 4) with $\tau \to \infty$. Similar to the mating functions above, we calculated the number of matings for each $f = 1, 11, 21, ..., 191, 200$ females and $m = 1, 11, 21, ..., 191, 200$ males for $\alpha = 0, -0.5, -1, -10, -\infty$ and $\beta = 0.5$. The end result is the mating function $\mathfrak{B}_{\mathrm{h}}$ as a function of the number of females (f), number of males (m), and shape parameter α.

Spatial spread framework

Next, to describe the growth and spatial spread of the population, we use the two-sex integrodifference equation model developed by Miller *et al.* (2011). We now track the densities of females and males at location x and time t, given by $f_t(x)$ and $m_t(x)$, respectively. Time is discrete (t is an integer) and space is continuous (x is any real number). Although most organisms move in at least

two spatial dimensions of habitat (and indeed we simulate mating dynamics in two dimensions as described above), here we simulate spatial spread in a single dimension for simplicity.

Four processes (dispersal, mating, reproduction, and survival) occur sequentially to determine the number of individuals at the next time step $(t+1)$. First, individuals disperse, with potentially different dispersal kernels for females and males, given by $k_{\mathrm{f}}(x,y)$ and $k_{\mathrm{m}}(x,y)$, respectively. The dispersal kernel describes the probability of an individual from any given starting location y dispersing to any given ending location x. For the purposes of this paper we assume the dispersal kernels only depend on the absolute distance travelled, so we may write the kernel as functions of a single variable, i.e., $k_{\mathrm{f}}(|x-y|)$ and $k_{\mathrm{m}}(|x-y|)$. Second, males and females mate, and the total number of matings at each location x is given by the mating function $\mathfrak{B}(f(x),m(x))$ (described in the previous section). Note that mating occurs locally (Fig. 1). Third, each mating produces ϕ female and μ male offspring. Finally, only a fraction of offspring survive, given by the density-dependent function g. Generally we assume that g decreases with increasing adult population size, so that

$$g(0,0) = 1 \tag{6a}$$

$$\frac{\partial g}{\partial f} \leq 0 \tag{6b}$$

$$\frac{\partial g}{\partial m} \leq 0 \tag{6c}$$

for all $f, m \geq 0$. These assumptions preclude Allee effects acting through this component of the model. In our simulations, we use the same density dependence

function used by Miller *et al.* (2011),

$$g = \frac{b}{b + m + f} \ , \tag{7}$$

where b is the population density at which survival is reduced by 50% due to density dependence. Adults die after reproduction, so generations are non-overlapping.

Bringing together all of these processes gives the full model

$$f_{t+1}(x) = \phi g\Big[k_{\mathrm{f}}(x) * f_t(x), k_{\mathrm{m}}(x) * m_t(x)\Big]\mathfrak{B}\Big[k_{\mathrm{f}}(x) * f_t(x), k_{\mathrm{m}}(x) * m_t(x)\Big] \tag{8a}$$

$$m_{t+1}(x) = \mu g\Big[k_{\mathrm{f}}(x) * f_t(x), k_{\mathrm{m}}(x) * m_t(x)\Big]\mathfrak{B}\Big[k_{\mathrm{f}}(x) * f_t(x), k_{\mathrm{m}}(x) * m_t(x)\Big] \tag{8b}$$

where "$*$" denotes a convolution operator, defined as

$$k(x) * n(x) = \int_{-\infty}^{\infty} k(x - y)n(x)\ dy \ . \tag{9}$$

We numerically simulated model (8) with the different mating functions ($\mathfrak{B}_{\mathrm{u}}$, $\mathfrak{B}_{\mathrm{m}}$, $\mathfrak{B}_{\mathrm{f}}$, $\mathfrak{B}_{\mathrm{p}}$, $\mathfrak{B}_{\mathrm{a}}$, $\mathfrak{B}_{\mathrm{h}}$) and examined the invasion dynamics. To run a spatial simulation, we started with an initial density of 0.5 for each sex for $|x| < r$ and 0 elsewhere (dashed-dotted line in Fig. 1). Here we used Gaussian dispersal kernels with mean 0 and variance v_{f} for females and v_{m} for males, and ran simulations for 100 generations. We defined the edge of the population as the first location where the population density was above the threshold value of 0.01. We then calculated the rate of population spread as the difference between the location of the edge of

the population from one time step to the next.

For comparison, we also simulated a simplified version of model (8) without dispersal or space, given by

$$f_{t+1} = \phi g\Big[f_t, m_t\Big]\mathfrak{B}\Big[f_t, m_t\Big] \tag{10a}$$

$$m_{t+1} = \mu g\Big[f_t, m_t\Big]\mathfrak{B}\big[f_t, m_t\Big] \ . \tag{10b}$$

For these simulations, we calculated the per capita growth rate as

$$R = \frac{f_{t+1} + m_{t+1} - (f_t + m_t)}{f_t + m_t} \tag{11}$$

in order to examine how the different mating functions affect population growth, varying both the amounts of time allowed for mate searching (τ) in the mating functions, as well as the initial population radius (r).

Hybrid framework

Finally, we link the mating functions developed in the *Mating dynamics* section (described in terms of discrete numbers of individuals and matings) with the spatial spread framework developed in the *Spatial spread framework* section (described in terms of continuous densities), into a hybrid framework. To do so, we first divide each of the mating functions (which give the number of matings as a function of the numbers of males and females) by the area considered (100 patches of 1 unit area each) to get the density of matings as a function of the densities of

males and females. Next, we use linear interpolation to generate estimates of mating density for male and female densities that fall between the values that we simulated. Finally, we generate estimates of mating density for male and female densities that fall outside the range of values that we simulated (below 0.01 or above 2.0). Here we consider two different case: plateauing and extrapolating.

As a default, we assume that the number of matings plateaus at both low and high densities. When either the value of f or m falls below the lowest value in the mating function (0.01) at a location y, we assume that no matings occur at that location (i.e., $\mathfrak{B}(f(y), m(y)) = 0$). When both the values of f and m fall above 2 (the highest value in the mating function) at a location y, we assume that the maximum number of matings found in the mating function occur ($\mathfrak{B}(f(y), m(y) = \max_{f,m}(\mathfrak{B})$). When just $f > 2$, we determine matings based on the m value and $f = 2$. Similarly, when just $m > 2$, we determine matings based on the f value and $m = 2$.

For comparison, we also considered the case where there is no bound on the number of matings at either low or high density. When either the value of f or m falls below the lowest value in the mating function, we use linear extrapolation with $\mathfrak{B}(0, m) = \mathfrak{B}(f, 0) = 0$ to estimate the matings that occur. When either the values of f or m fall above the highest value in the mating function, we assume that $\min(f, m)$ matings occur.

Results

We first calculated the number of matings according to each mating function, then we examined how each mating function affects the population growth rate in

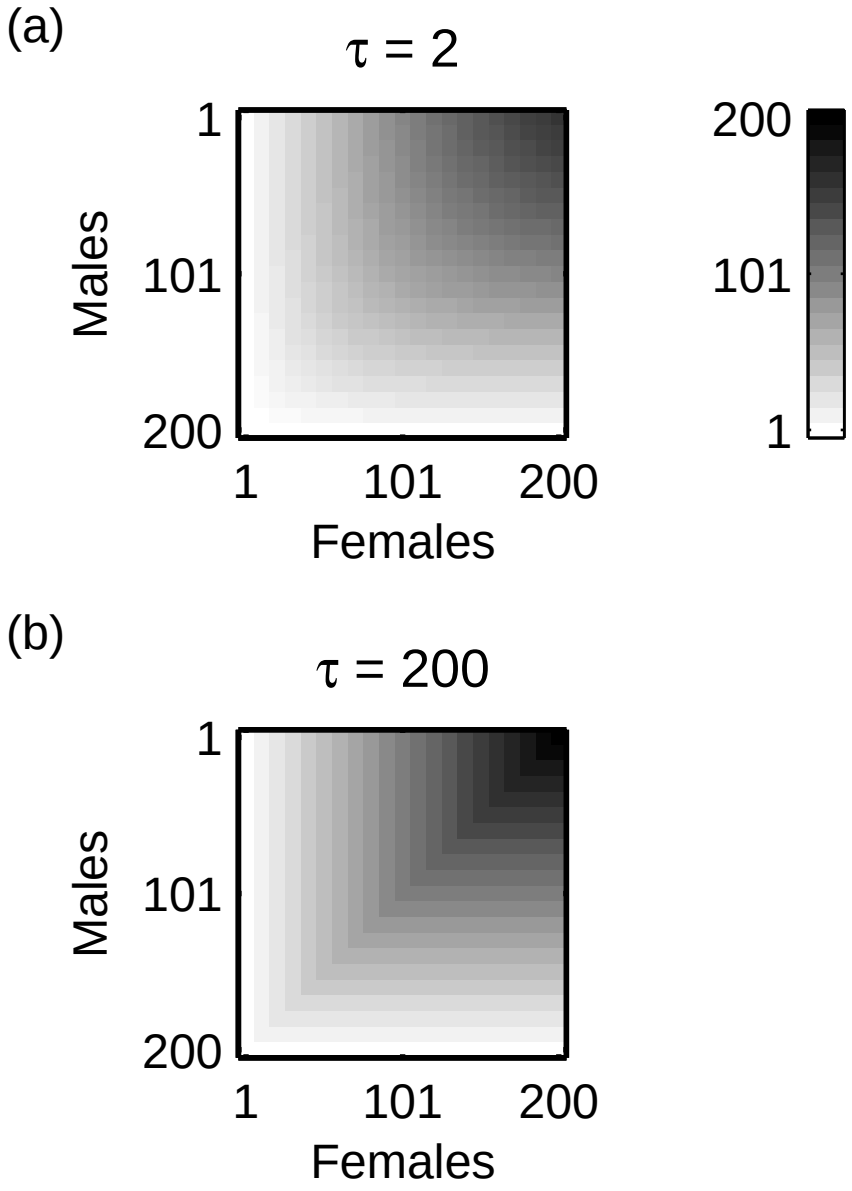
a non-spatial model, and finally we determined how each mating function affects the establishment probability and the subsequent rate of spread in the full spatial model.

Mating dynamics

Intuitively, increasing the number of males, the number of females, or the time allowed for pair formation increased the number of mated pairs that formed. This was true for mating function $\mathfrak{B}_{\mathrm{u}}$ (individual-based mating function with equal searching by males and females), as well as the sex-biased mate searching mating functions, $\mathfrak{B}_{\mathrm{f}}$ and $\mathfrak{B}_{\mathrm{m}}$ (Figs 2, S1a-c). There was also essentially no difference between the number of matings produced by $\mathfrak{B}_{\mathrm{f}}$ and $\mathfrak{B}_{\mathrm{m}}$ (Fig. S1b-c). Sex-biased searching produced the same number of matings as unbiased searching when the sex ratio was skewed, and fewer matings when the sex ratio was close to even (Fig. S1d-e). The mating function $\mathfrak{B}_{\mathrm{p}}$ (polygynandrous mating) approaches f for large τ (Fig. S2a). The mating function $\mathfrak{B}_{\mathrm{a}}$ (mass action) produced essentially the same number of matings as $\mathfrak{B}_{\mathrm{u}}$ (Fig. S2). Although the $\mathfrak{B}_{\mathrm{h}}$ (Hölder means) mating function does not include search time explicitly as a parameter, shifting α more negative produces qualitatively similar results as increasing the search time τ in the individual-based mating function (Figs S1a, S2c). The Hölder means, however, overestimated the number of mates at low densities and for short search times (Fig. S2e).

Each mating function meets the criteria described by Courchamp, Berec & Gascoigne (2008) for a mate-finding Allee effect. That is, the female mating rate $P(f, m)$ (or fraction of females that are mated) satisfies the following four proper-

Figure 2: A contour plot of the number of pairs formed as a function of the number of females and males present, for the unbiased mating function ($\mathfrak{B}_{\mathrm{u}}$), for $\tau = 2$ and $\tau = 200$ (the number of time steps allowed for pair formation). Mating functions were calculated using the mate search shape parameter $a = 5$.



ties:

1. "There is no mating if there are no males: $P(f, 0) = 0$ for any f.

2. For a given number of females, a female's probability of mating (or mating rate) cannot decrease if the number of males increases: $P(f, m)$ is a non-decreasing function of m for any fixed f.

3. For a given number of males, a female's probability of mating (or mating rate) cannot increase if the number of females increases: $P(f, m)$ is a non-increasing function of f for any fixed m.

4. If males greatly outnumber females, mating is virtually certain for females: $P(f, m)$ approaches 1 for a sufficiently large m/f ratio."

Note, however, that most verbal definitions of a mate-finding Allee effects describe it as a difficulty or failure to find mates at low density, or a limited amount of time available for mating (Dennis, 1989; Stephens, Sutherland & Freckleton, 1999; Calabrese & Fagan, 2004). Although the criteria above describe how a female's mating probability should change as the density of each males and females change separately, they do not provide a description of how mating probability changes with overall changes in population density (with a fixed sex ratio). Therefore we recommend that a fifth criterion be added:

5. At low density, equally increasing the number of males and females present should increase a female's probability of mating (or mating rate): $P(af, am) > P(f, m)$ for small f and m, and $a > 1$.

With this added criterion, the minimum mating function (and the general Hölder means mating function) does not display a mate-finding Allee effect, since a fe-

male's probability of mating remains constant as male and female density increase proportionally. Our classification of the minimum mating function is in line with verbal statements of mate-finding Allee effects, which typically require some form of limitation (due to low population density or short mating time) not present in the minimum mating function.

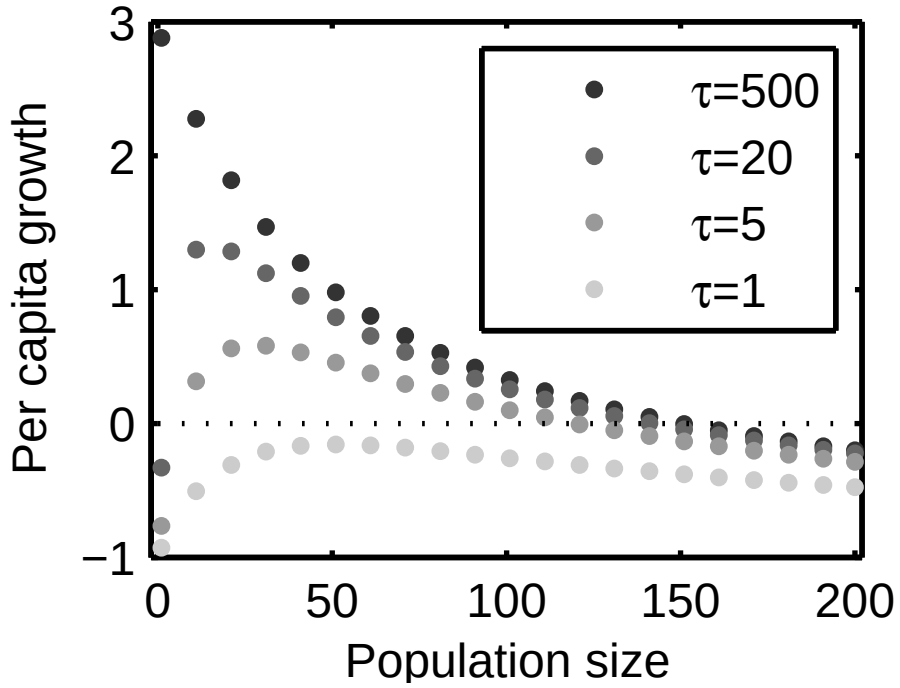
Non-spatial dynamics

Simulations of the non-spatial model (10) show that for short search times (low τ), the unbiased individual-based mating function exhibits a demographic Allee effect, i.e., the per capita growth rate increases with population size, for small populations (Fig. 3). This demographic Allee effect is more pronounced for shorter mate search times (smaller τ), thus τ is effectively an indicator of the Allee effect strength. A population with very short search times ($\tau = 1$) does not grow; the per capita growth is always negative. For very long search times ($\tau = 500$), there is no demographic Allee effect, i.e. the per capita growth decreases monotonically with population size. The other individual-based mating functions (male-biased, female-biased and polygynandrous) all show qualitatively the same patterns as the unbiased individual-based mating function. Similarly, the mass action mating function contains a demographic Allee effect for shorter search times (smaller $c\tau$), and no demographic Allee effect for large search time.

Establishment

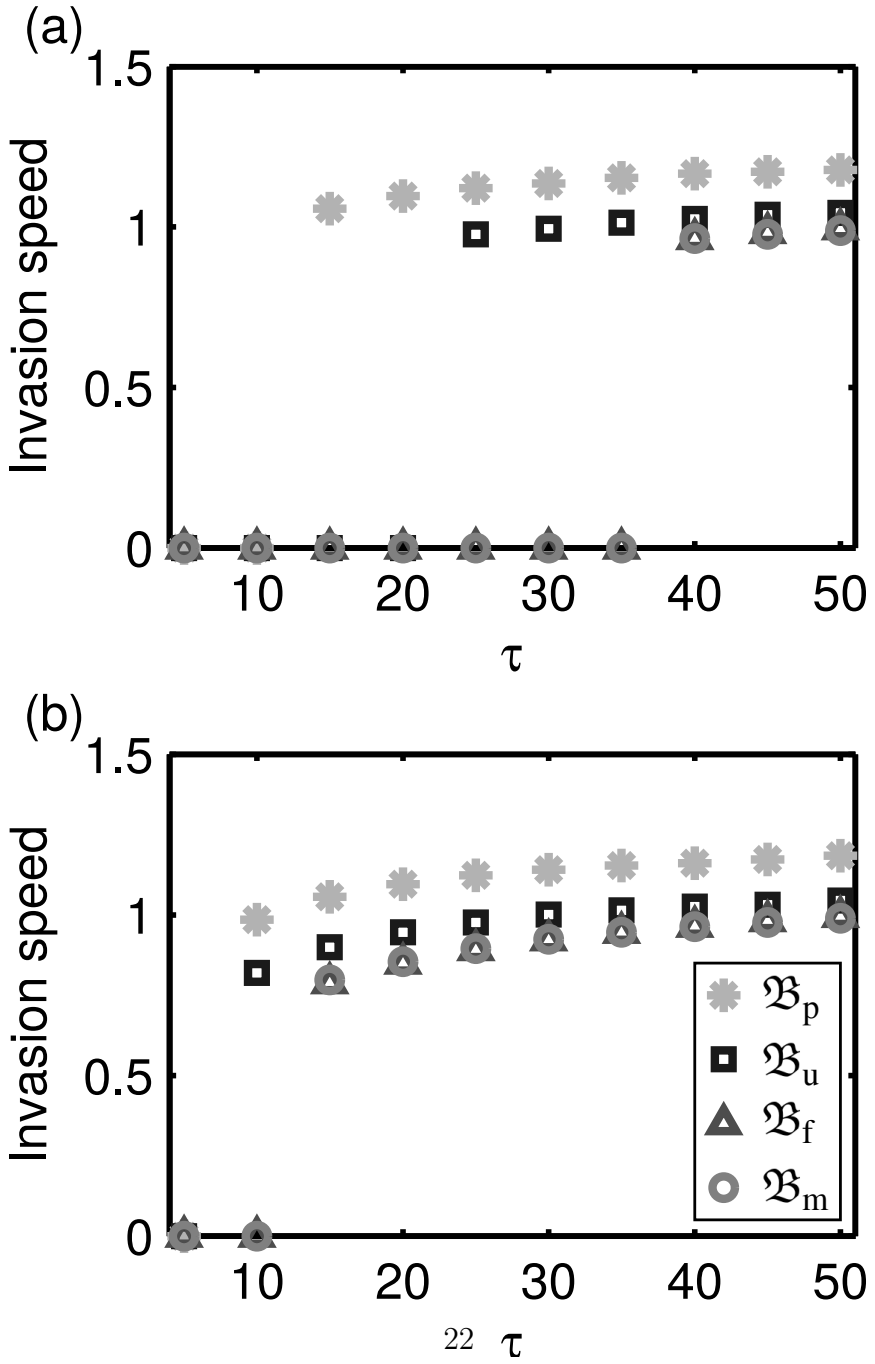
In the spatial spread simulations, populations were only able to establish if they had a sufficiently high initial density, and if individuals could search for sufficiently

Figure 3: The per capita growth rate (eqn. 11) as a function of population size, for simulations of the non-spatial model (eqn. 10) with $b = 100$, $\mu = \phi = 4$, $m = f$ and the individual-based mating function with unbiased searching ($\mathfrak{B}_u$) and different values of search time, τ.



long mate-search times (τ). The effect of these two conditions was interactive: for larger initial populations, a shorter mate-search time was required for the population to establish (Fig. 4a vs b). This was true for each of the individual-based mating functions (Figs 4, S5). Below a threshold mate-search time and/or initial density, the population failed to establish and went extinct, indicating a strong mate-finding Allee effect. The threshold mate-search time, below which populations went extinct, was higher in spatial simulations than non-spatial simulations. Populations with polygynandrous mating were able to establish under the broadest range of conditions, followed by those with unbiased mating; male-

Figure 4: The long-term invasion speed (averaged across generations 90 to 100) as a function of search time (τ) for (a) initial population radius of $r = 0.15$ and (b) $r = 0.3$, for each of the individual-based mating functions: polygynandrous ($\mathfrak{B}_{\mathrm{p}}$, stars), unbiased ($\mathfrak{B}_{\mathrm{u}}$, squares), female-biased ($\mathfrak{B}_{\mathrm{f}}$, circles), and male-based ($\mathfrak{B}_{\mathrm{m}}$, triangles). Simulations were run with parameters $b = 1$, $v_{\mathrm{m}} = v_{\mathrm{f}} = 1$ and $\mu = \phi = 4$.

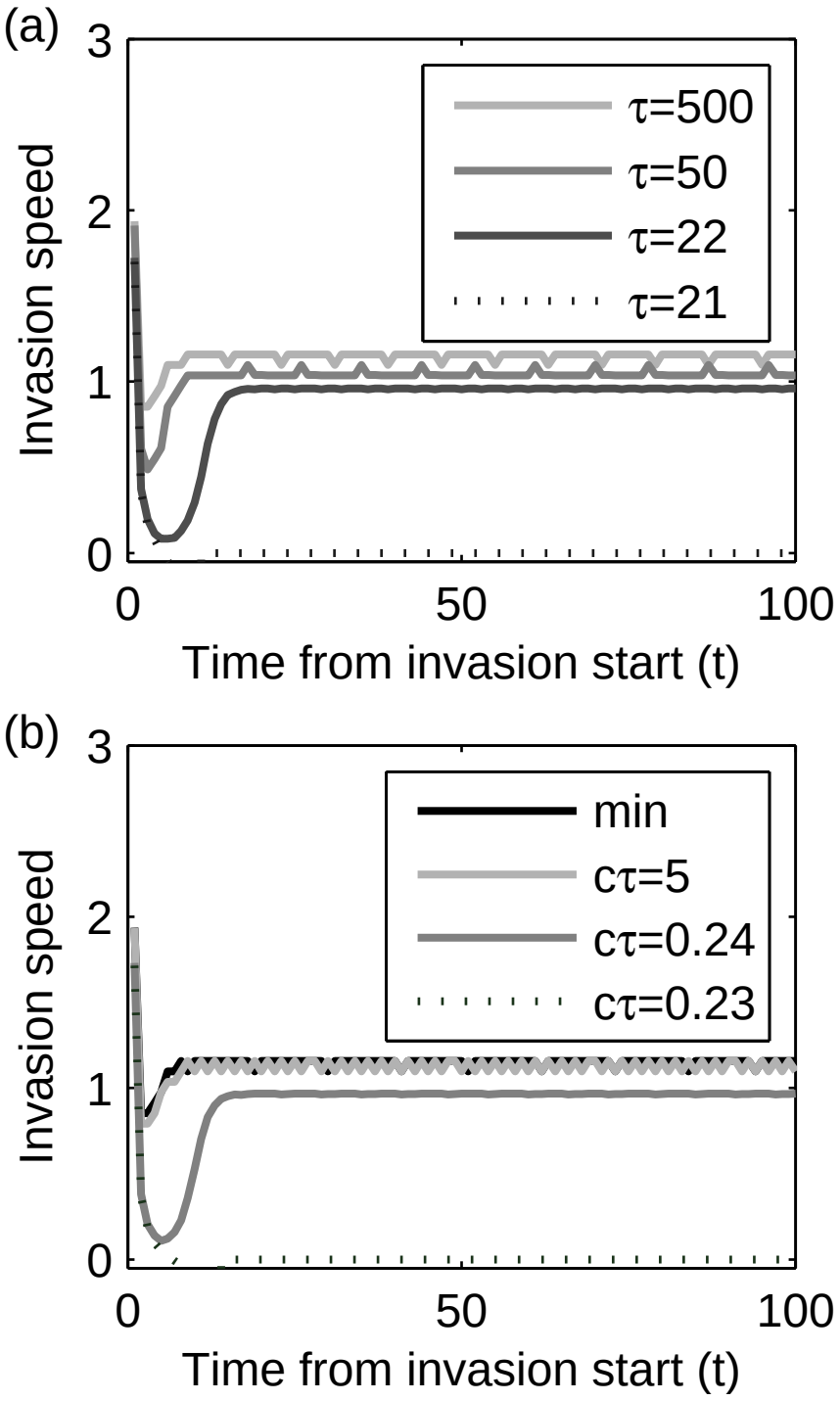


and female-biased mating populations established under the narrowest range of parameter values. Populations with the mass action mating function similarly had a threshold below which they were not able to establish (Fig. S5). The mass action establishment patterns most closely matched those of the unbiased individual mating function. However, populations with the Hölder means mating function were always able to establish and spread, for the range of parameters considered (Fig. S5). Extrapolating the number of matings that occurred at low and high population densities (instead of assuming that the number of matings plateaued) increased the range of conditions where populations could establish (Fig. S6 vs. S5).

Rate of spread

For populations that did successfully establish, the initial population density and mate-search time also affected the spread dynamics. For simulations with the unbiased mating function, the population spread rate started high, dropped to a lower speed, then accelerated to an intermediate rate of spread, which was maintained over time (Fig. 5a). Generally, for larger τ and larger initial densities, both the very initial rate of spread and the lowest spreading speed were higher (Figs S3, S4). For larger τ, the transient acceleration period was shorter and the long-term rate of spread was faster, whereas initial population density had little effect on the long-term spread rate (Fig. S5). Simulations with the male- and female-biased mating functions always spread slightly slower than unbiased mating function simulations, for the same value of τ (Fig. 4). In contrast, simulations with the polygynandrous mating functions always spread faster than those with

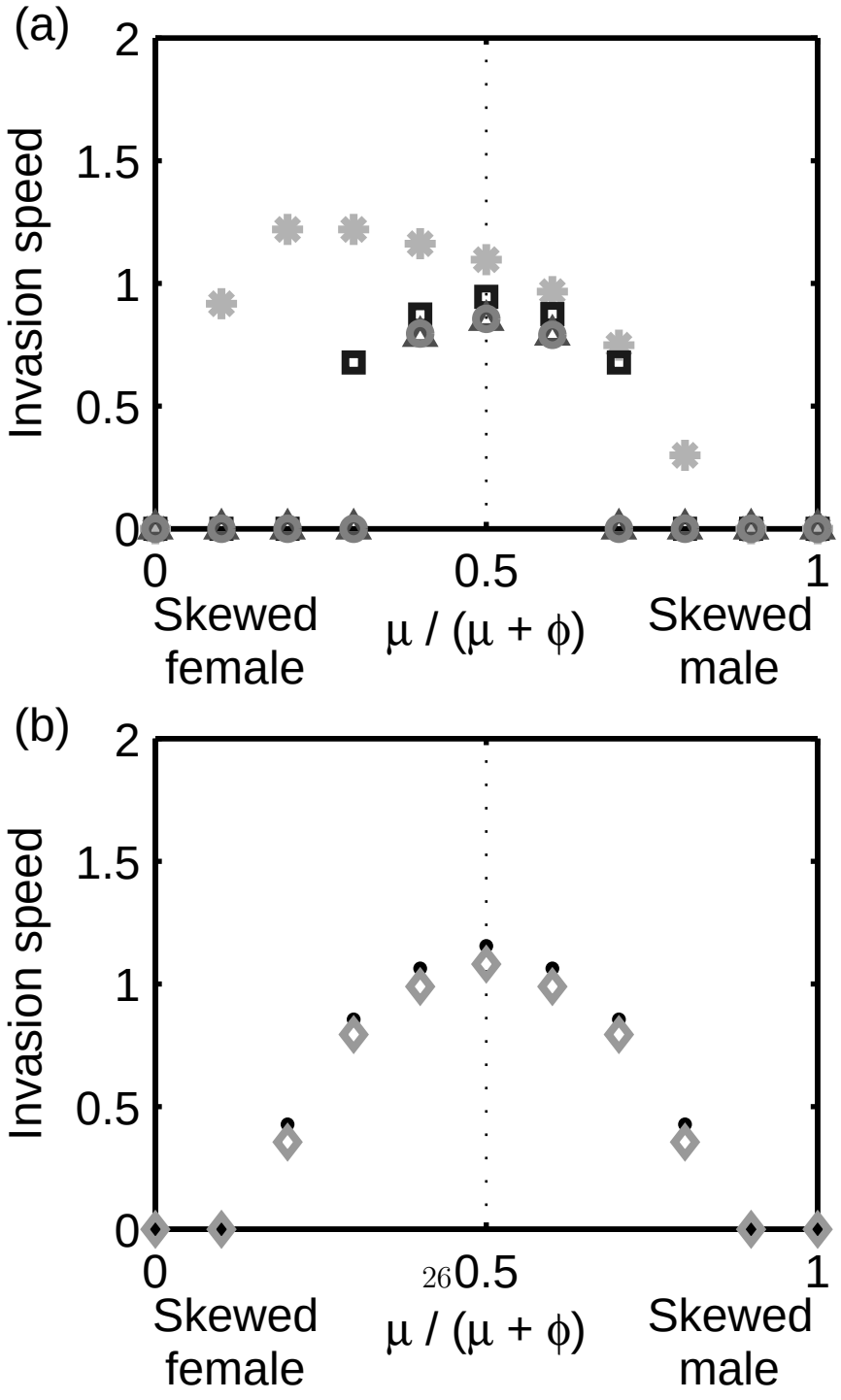
Figure 5: The invasion speed over time for simulations with (a) the unbiased mating function, $\mathfrak{B}_{\mathrm{u}}$, and (b) the Hölder means ($\mathfrak{B}_{\mathrm{h}}$) and mass action ($\mathfrak{B}_{\mathrm{a}}$) mating functions. Parameters: $b = 1$, $r = 0.15$, $v_{\mathrm{m}} = v_{\mathrm{f}} = 1$, $\mu = \phi = 4$.



the unbiased mating function, for the same value of τ. A number of simulations (particularly for large τ) had slight fluctuations in invasion speed, even during during the long-term rate of spread (Fig. 5). Simulations with the mass action mating function produced similar results, with populations spreading slowly before switching to a faster rate of spread (Fig. 5b). For longer mate-search times ($c\tau$), the period of slow spread was shorter and the long-term rate of spread was faster, and there were slight fluctuations in the long-term spread rate. Simulations with the Hölder means mating function with $\alpha = -\infty$ and $\beta = 0.5$ (the minimum mating function) produced dynamics similar to simulations with the unbiased mating function and long mate-search times (Fig. 5b). Simulations where the number of matings was extrapolated at low and high population densities spread slightly faster than those where the number of matings plateaued, and also did not have any fluctuations in the long-term rate of spread (Fig. S7 vs 5).

Finally, we considered how sex differences in life history parameters influenced the invasion speed. Here we considered both a skew in sex ratio and sex differences in dispersal distance. A skewed sex ratio could be the result either of sex ratio bias at birth, or (more likely) of mortality differences among juveniles. For all mating functions, as skew in sex ratio at birth increased towards either male or female (holding the total number of offspring produced per female constant), the spread rate generally decreased, with a threshold beyond which the invasion failed (Fig. 6). As with earlier results for the individual-based simulations, populations with the male-biased and female-biased mating functions were able to establish under the narrowest range of parameter values and spread the slowest, followed by unbiased mating functions, with polygynandrous simulations able to spread across the broadest range of conditions and producing the fastest rates of spread (Fig.

Figure 6: The long-term invasion speed (averaged across generations 90 to 100) as a function of the skew in sex ratio calculated from simulations with the (a) polygynandrous ($\mathfrak{B}_{\mathrm{p}}$, stars), unbiased ($\mathfrak{B}_{\mathrm{u}}$, squares), female-biased ($\mathfrak{B}_{\mathrm{f}}$, circles), and male-based ($\mathfrak{B}_{\mathrm{m}}$, triangles), individual-based mating functions, and (b) the mass action mating function ($\mathfrak{B}_{\mathrm{a}}$, diamonds), and the Hölder means mating function ($\mathfrak{B}_{\mathrm{h}}$, dots). Parameters: $\tau = 20$ (individual-based), $c\tau = 1$ (mass action), $\alpha = -\infty, \beta = 0.5$ (Hölder), $b = 1$, $r = 0.2$, $v_{\mathrm{m}} = v_{\mathrm{f}} = 1$ and $\mu + \phi = 8$.



6a).

Populations simulated with the mass action and Hölder means mating functions produced qualitatively similar results as the unbiased individual-based mating function (Fig. 6b). The polygynandrous mating function was the only one that produced invasion speeds that were asymmetric for male versus female skew in the life history parameters. These simulations spread much faster for female-skewed populations compared to male-skewed ones, presumably because when individuals can mate multiply, sperm (or pollen) is not often limited, whereas the number of mated females becomes the limiting factor for population growth and spread.

Skewed sex bias in dispersal (holding the average dispersal distance in the population constant) resulted in qualitatively similar patterns as skewed sex ratio (Fig. S8). Although skewed sex ratio and sex bias in dispersal each alone reduced the rate of spread, combining the two increased the invasion speed in some cases. This occurred only when the skew for each was in opposite directions (e.g., male-biased sex ratio coupled with female-biased dispersal, or female-biased sex ratio coupled with male-biased dispersal) and for very small degrees of bias in each (Fig. S9).

Discussion

Here we have developed a hybrid approach that links individual mating behaviour to populations dynamics, in a two-sex spreading population. This approach enables us to include key aspects of two-sex populations: sex differences in demographic and dispersal parameters, and the mechanics of locating mates. We modelled the mate-search process assuming that only males, only females, or both sexes

searched for mates, and with monogamous pairs or polygynandrous mating. We determined how these different mating scenarios affected the number of matings, the per capita growth rate, the ability of a population to establish from low density, and the dynamics and rate of population spread. Finally, we compared results from the individual-based mating functions to results from two mating function approximations.

Mate-search efficiency, which we here model as the amount of time that individuals had to search for mates (τ) was a key parameter driving population-level outcomes. For low values of τ, there was a strong demographic Allee effect, where the population was not able to grow from low densities. For slightly larger values of τ, a non-spatial population that grew without spreading was able to establish, while adding spatial spread caused establishment to fail. (Note that this is a typical result for spatial spread with an Allee effect; Lewis & Kareiva 1993; Goodsman & Lewis 2016.) For larger values of τ, the demographic Allee effect became weaker, and the population was able to establish in both spatial and non-spatial contexts, but went through a long transient phase of slow spread before switching to a faster long-term spread rate. For even larger values of τ, the demographic Allee effect vanished, the slow phase of population spread was quite short, and the long-term rate of spread was quite fast. These results held within each of the individual-based mating functions considered: male- or female-biased mate searching with monogamous pair formation, and unbiased mate searching with monogamous pairs or polygynandrous mating. However, populations with sex-biased mate searching were the least robust, failing to invade for conditions under which unbiased mate searching populations were successfully able to invade, and spreading at a slower rate when they were able to invade. In contrast, populations with polygynandrous

mating were the most robust, able to spread in conditions where populations with each of the monogamous mating functions were not able to establish. Initial population density had some interactive effects with mate search time: populations that started at too low a density failed to establish, and as initial population density increased the threshold mate search time required for establishment decreased.

The dynamics were to some extent found to be different between the individual-based mating functions and the approximations. This is unsurprising per se, as approximations do not perfectly capture the mating dynamics in the IBM, but it is worthwhile to comment on when precisely large failures were found. The mass action mating function was a good proxy for the case of monogamous mating if searching had no sex bias, but it performed less well if searching was sex-biased or if matings were polygynandrous. The Hölder means mating function was only a good proxy for the monogamous mating function for very large search times (big τ). Even though the effect of the Hölder means' α parameter on the number of matings was qualitatively similar to increasing search time τ in the individual-based simulations, the Hölder means mating function did not display any of the Allee threshold behaviour that was characteristic of the dynamics of the individual-based mating functions. The Hölder means mating function also shared the property of the mass action function that it did not form a good proxy when searching was sex-biased or there was polygynandry. For these reasons, some dynamic effects were only discoverable using the IBM.

Some of our simulations showed fluctuations in the long-term invasion speed, beyond the initial period of slow spread. The fluctuations were only noticeable if we assumed that the number of matings plateaued at low and high densities (rather than linearly extrapolating the number of matings at low and high densities). At

low densities, this is the equivalent to imposing a strong mate-finding Allee effect (a threshold density below which no matings, and therefore no population growth, occurs). However, a strong mate-finding Allee effect alone is not sufficient to generate these oscillations. For comparison, we ran simulations with a minimum mating function that was calculated exactly at all densities (no interpolation) but with a threshold density below which no matings occurred. These simulations produced smaller oscillations (Fig. S10), suggesting that oscillations are caused by some combination of a strong mate-finding Allee effect and the nonlinearities introduced by interpolating the mating function at intermediate densities. Recent work on oscillations in invasion speed in one-sex models supports this idea (Sullivan et al. unpublished).

Our findings broadly align with past empirical and theoretical work demonstrating that Allee effects can prevent (Lewis & Van Den Driessche, 1993; Goodsman & Lewis, 2016), slow (Lewis & Kareiva, 1993; Taylor & Hastings, 2005; Tobin *et al.*, 2007; Krkošek *et al.*, 2012) or delay (Hopper & Roush, 1993; Kot, Lewis & van den Driessche, 1996; Veit & Lewis, 1996) population spread. The novelty of our study is showing how the details of individual behaviour determines the impact of a mate-finding Allee effect. Our work also builds on the models of Miller *et al.* (2011) and Shaw & Kokko (2015), which separately examined the influence of sex-biased dispersal and of mating dynamics, respectively. Here we have shown that sex-specific life history traits (like sex-biased dispersal) interact with mating mechanics, typically resulting in both a reduced invasion probability and a slower invasion speed. The exception is when individuals can mate multiple times and when life history traits are skewed female (females disperse farther or female-skewed sex ratio): with this combination the population spreads faster than

a population with only one of these factors. We have also shown that different sex-specific life history traits have compensatory effects on invasion speed: skewed sex ratio and sex-biased dispersal alone each slow an invasion, but a male-skewed sex ratio combined with female-biased dispersal (and vice versa) can speed up an invasion.

Our model describes mate-finding difficulties by altering the time, τ, available for individuals to search before they have to give up and remain unmated (for life, as ours is a discrete generation model). The longer the time is, the wider the area that the individuals can search, thus τ in our model can be interpreted in several possible ways, broadening the scope of the model from the narrowest interpretation that τ must be measured in units of time. Under a more general view, high τ reflects mate-search efficiency that can be brought about by efficient locomotion and/or high sensory capacities to locate mates that are relatively far away. For example, male *Lymantria dispar* (gypsy moths) find females that emit pheromones; interestingly, despite mate searching therefore presumably being relatively efficient, it still is not efficient enough to avoid Allee effects at range boundaries (Contarini *et al.*, 2009). Fish lice (parasites of fish) such as *Lepeophtheirus salmonis* also appear to be intermediate cases: males disperse among fish in search of mates, but again, this is not efficient enough to avoid mate-finding Allee effects (Krkošek *et al.*, 2012).

When do we expect τ to be low enough in natural systems to cause mate-finding Allee effects? Our model is not evolutionary (τ does not evolve), but evolutionary ideas can help elucidate when invasion speeds are likely to be negatively impacted by mate availability. If females in the core of their range do not remain unmated, τ is 'large enough' (i.e., leads to high female fertilization rate) under these conditions.

Newly established populations may then 'use' the same value for τ even if it now leads to poorer mating success — either because there's not sufficient heritable variation present to lead to improved behaviours, or because of gene flow from the core range importing behaviours that create a too low τ for the local conditions. We should note, however, that not all marginal populations necessarily experience mate-finding difficulties (Fauvergue & Hopper, 2009); a possible cause is that range margins might maintain high local densities despite being more fragmented (Gaston 2009, however note that this paper is not focused on an explicit invasion context).

Mate-finding Allee effects are typically defined as a reduced ability, or failure, to find mates at low density (Dennis, 1989; Wells *et al.*, 1998; Stephens, Sutherland & Freckleton, 1999). Although there is consensus on this general definition, explicit criteria for determining whether a system displays a mate-finding Allee effect are rarely given. Courchamp, Berec & Gascoigne (2008) provide one such set of criteria: the probability of mating per female should increase (or be constant) as the number of males increases, and should decrease (or be constant) as the number of females increases. However, within this definition, the effect of an overall increase in density (with a constant ratio of males to females) on probability of mating per female is not specified. To address this deficiency, and to align the explicit criteria for mate-finding Allee effects with the general definition, here we propose that an additional criterion be included. Namely, we suggest that at low density, increasing the population density (while keeping the sex ratio constant) should increase a female's probability of mating. However, a number of commonly used mating functions violate this criterion, meaning they do not display a mate-finding Allee effect under our revised definition. Specifically, within the

demography literature, a mathematically desirable (albeit controversial; Iannelli, Martcheva & Milner 2005) property of any mating function is that it should be homogeneous of degree one (Yellin & Samuelson, 1974; Legendre, 2004), that is, changing the population size (with a constant ratio of males to females) changes the number of matings, proportionally. This is generally equivalent to stating that a female's probably of mating is independent of population size, which conflicts with the above general definition of a mate-finding Allee effect.

Future studies could expand on the methods we develop here in order to explore how details of individual behaviour influence population spread rates. First, a wider range of individual mate finding behaviour could be explored, such as using a deterministic (instead of probabilistic) stopping rule or using signalling or homing to locate mates (Vane-Wright & Boppre, 1993). Second, many organisms have other adaptations for alleviating mate-finding Allee effects, such as moving more frequently at low density (Kindvall *et al.*, 1998), storing sperm across mating seasons (Parker, 1970), and context-dependent sex determination (Becheikh *et al.*, 1998). Finally a wider range of interactions between mating and life history characteristics could be considered – e.g., although we explored the effects of polygynandrous mating and sex-biased searching, we did not explore the effect of both factors combined. Each of these mechanisms could be simulated to determine how they influence population growth and spread rate.

Acknowledgements

We thank W. Petry and D. Stanton for discussion of ideas, and L. Berec and one anonymous reviewer for manuscript feedback. This material is based upon work

supported by the National Science Foundation under Grant No. OISE-1159097 to AKS and Grant No. DEB-1145017 to MGN. We acknowledge the Minnesota Supercomputing Institute (MSI) at the University of Minnesota for providing resources that contributed to the research results reported within this paper. URL: http://www.msi.umn.edu

Authors' Contributions

AKS and MGN conceived the model idea. AKS developed the model, ran simulations and wrote the paper, with contributions from HK and MGN.

Data accessibility

Model code is available from the Dryad Digital Repository: http://doi.org/10.5061/dryad.39n4g (Shaw, Kokko & Neubert, 2016).

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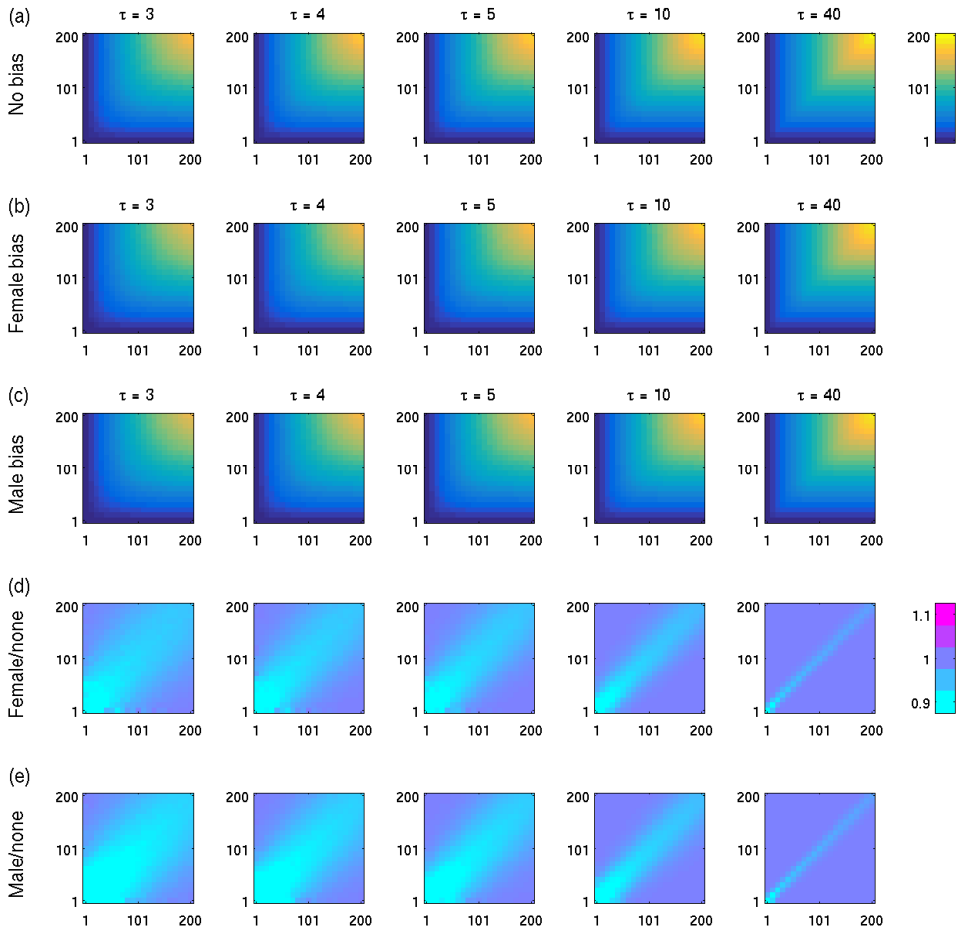

Figure 7: The number of pairs formed as a function of the number of females (x-axis) and males (y-axis) present, comparing across three different individual-based simulations for different values of τ (the number of time steps allowed for pair formation). (a) The number of pairs formed when both males and females search ($\mathfrak{B}_{\mathrm{u}}$). (b) The number of pairs formed when only females search and males are stationary ($\mathfrak{B}_{\mathrm{f}}$). (c) The number of pairs formed when only males search and females are stationary ($\mathfrak{B}_{\mathrm{m}}$). (d) The ratio between the values in (b) and (a). (e) The ratio between the values in (c) and (a). All mating functions were calculated using the mate search shape parameter $a = 5$.

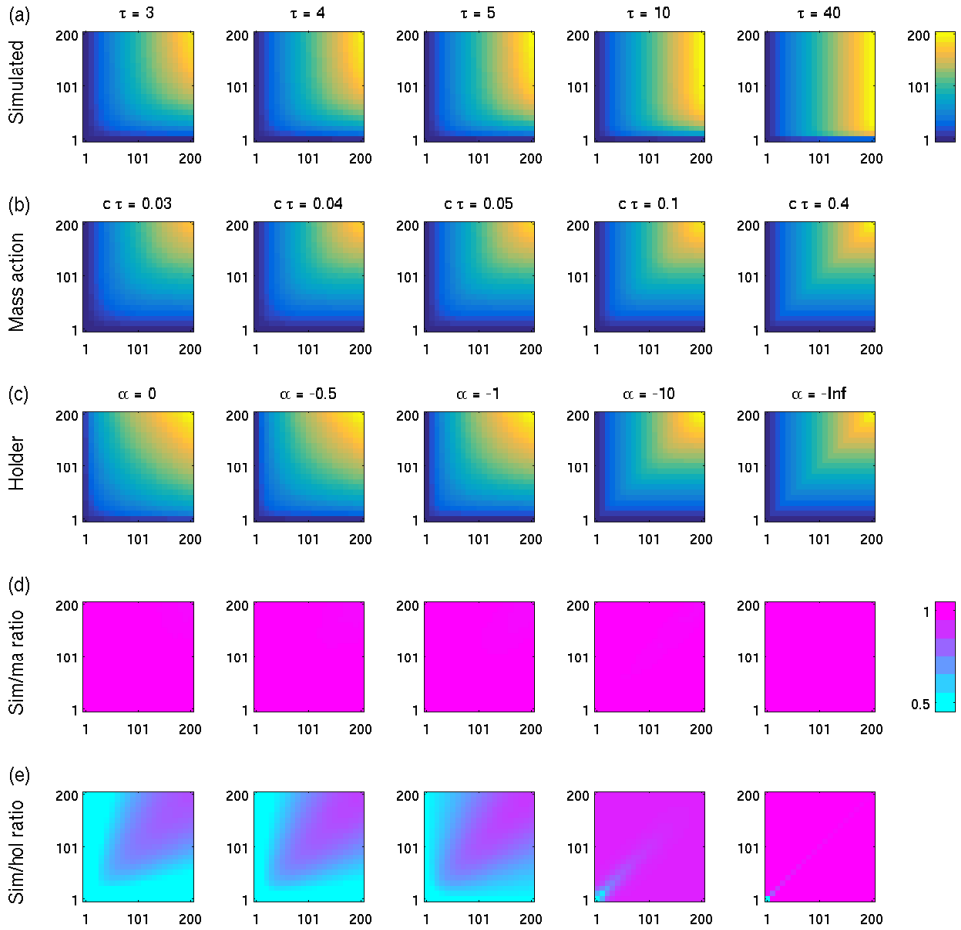

Figure 8: The number of pairs formed as a function of the number of females (x-axis) and males (y-axis) present, comparing across different mating functions. (a) The number of pairs formed in the individual-based mating function with polygynandrous mating ($\mathfrak{B}_{\mathrm{p}}$), for different values of τ (the number of time steps allowed for pair formation). (b) The number of pairs formed in the mass action mating function ($\mathfrak{B}_{\mathrm{a}}$) for different values of $c\tau$. (c) The number of pairs formed in the Hölder means mating function ($\mathfrak{B}_{\mathrm{h}}$) with $\beta = 0.5$ and different values of the shape parameter α. (d) The ratio between the values in Fig. S1a and (b) here. (e) The ratio between the values in Fig. S1a and (c) here. All mating functions were calculated using the mate search shape parameter $a = 5$.

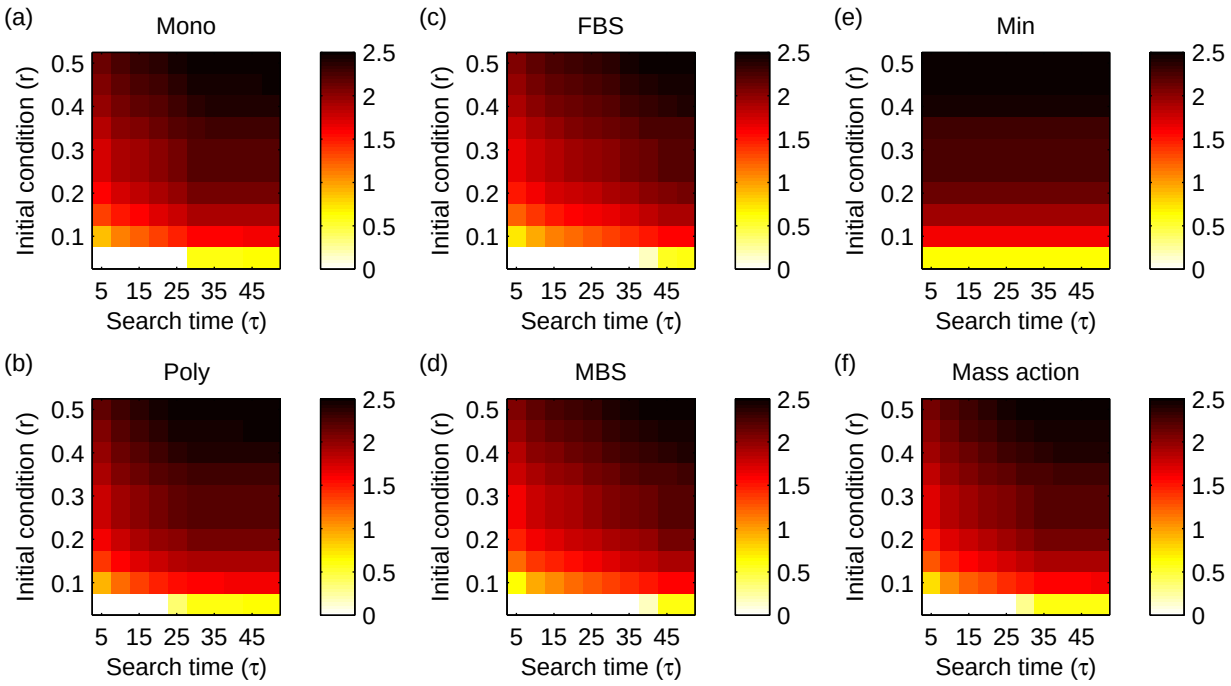

Figure 9: The initial invasion speed (generation 1) as a function of search time (τ) and the simulation initial population radius (r), for each of the mating functions. White regions indicate a failed invasion. Simulations were run with parameters $b = 1$, $v_{\mathrm{m}} = v_{\mathrm{f}} = 1$ and $\mu = \phi = 4$. The number of matings were assumed to plateau in the mating functions.

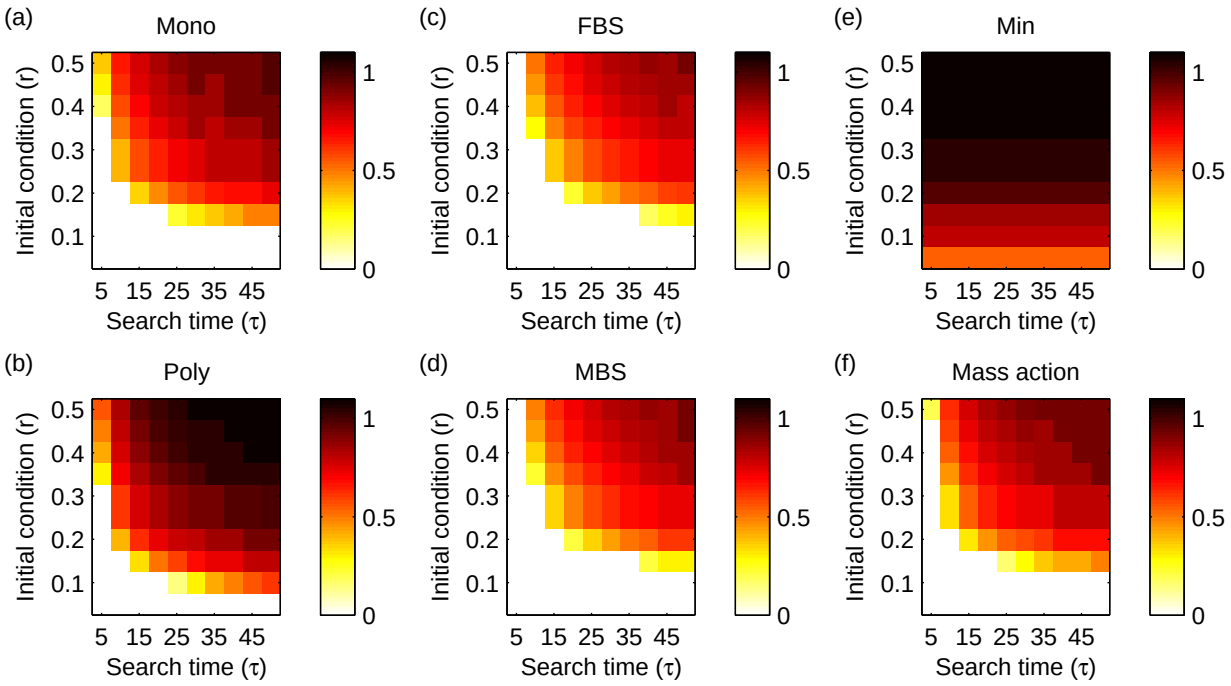

Figure 10: The minimum invasion speed as a function of search time (τ) and the simulation initial population radius (r), for each of the mating functions. White regions indicate a failed invasion. Simulations were run with parameters $b = 1$, $v_{\mathrm{m}} = v_{\mathrm{f}} = 1$ and $\mu = \phi = 4$. The number of matings were assumed to plateau in the mating functions.

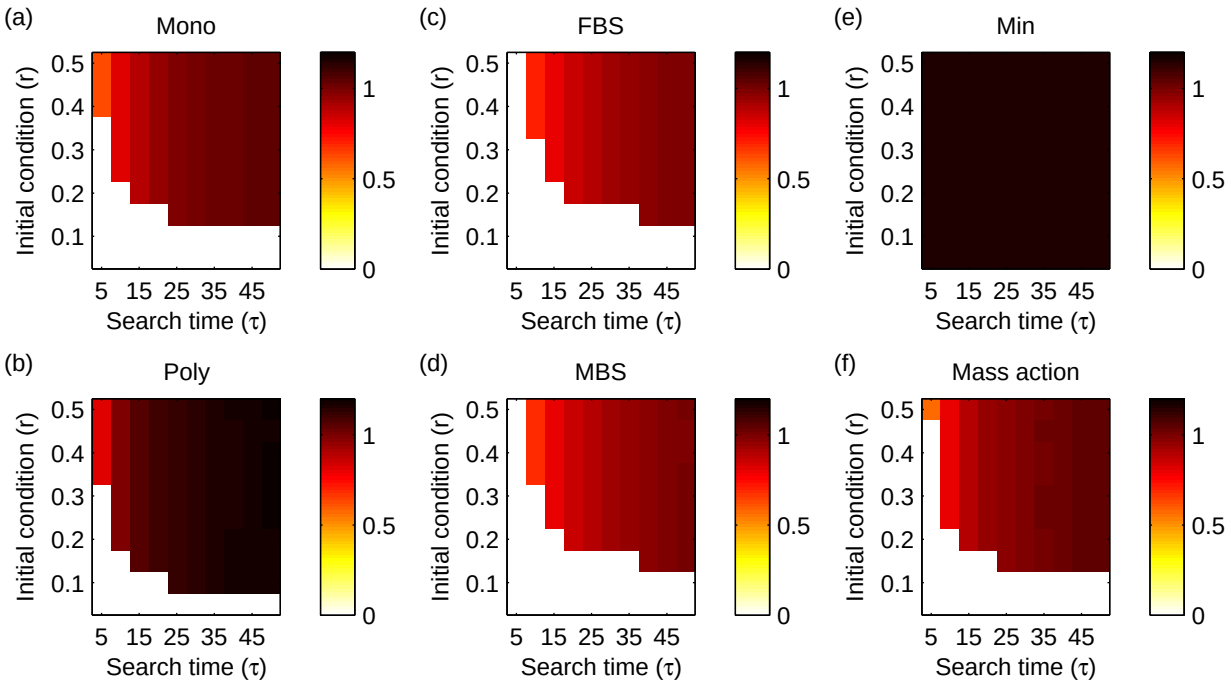

Figure 11: The long-term invasion speed (averaged across generations 90 to 100) as a function of search time (τ) and the simulation initial population radius (r), for each of the mating functions. White regions indicate a failed invasion. Simulations were run with parameters $b = 1$, $v_{\mathrm{m}} = v_{\mathrm{f}} = 1$ and $\mu = \phi = 4$. The number of matings were assumed to plateau in the mating functions.

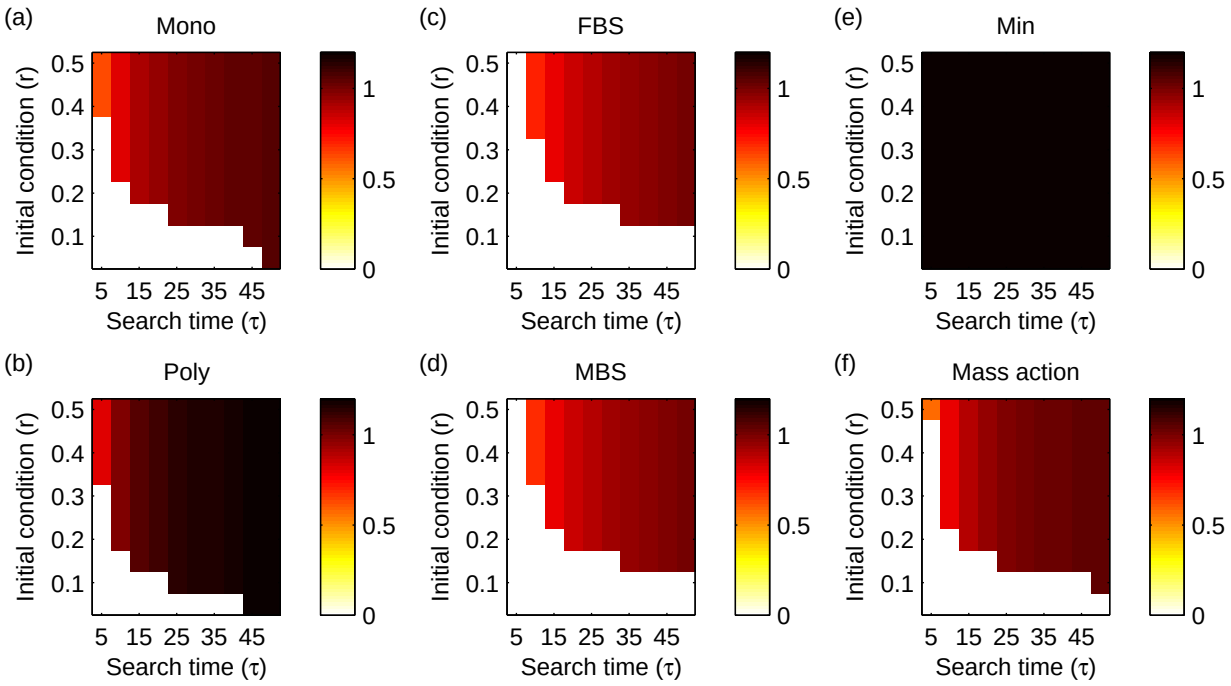

Figure 12: The long-term invasion speed (averaged across generations 90 to 100) as a function of search time (τ) and the simulation initial population radius (r), for each of the mating functions. White regions indicate a failed invasion. Simulations were run with parameters $b = 1$, $v_{\mathrm{m}} = v_{\mathrm{f}} = 1$ and $\mu = \phi = 4$. The number of matings were extrapolated at high and low densities in the mating functions.

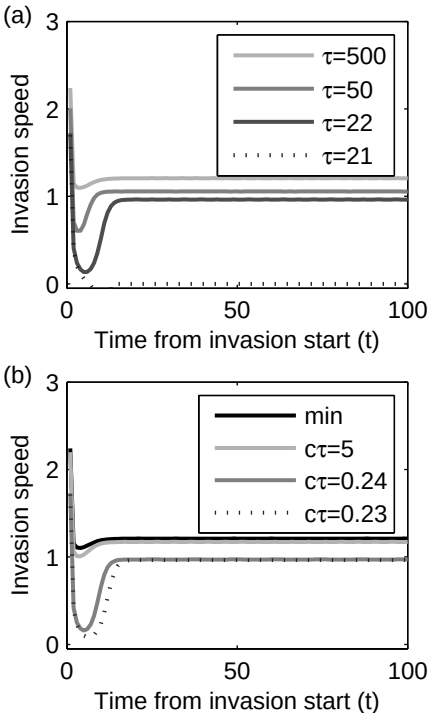

Figure 13: The invasion speed over time for simulations with (a) the unbiased mating function, $\mathfrak{B}_{\mathrm{u}}$, and (b) the Hölder means ($\mathfrak{B}_{\mathrm{h}}$) and mass action ($\mathfrak{B}_{\mathrm{a}}$) mating functions. Parameters: $b = 1$, $r = 0.2$, $v_{\mathrm{m}} = v_{\mathrm{f}} = 1$, $\mu = \phi = 4$. The number of matings were extrapolated at high and low densities in the mating functions.

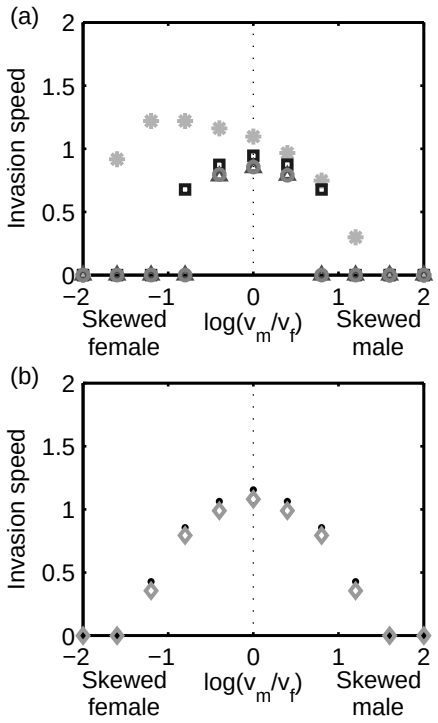

Figure 14: The long-term invasion speed (averaged across generations 90 to 100) as a function of the degree of sex bias in dispersal, calculated from simulations with the (a) polygynandrous ($\mathfrak{B}_{\mathrm{p}}$, stars), unbiased ($\mathfrak{B}_{\mathrm{u}}$, squares), female-biased ($\mathfrak{B}_{\mathrm{f}}$, circles), and male-based ($\mathfrak{B}_{\mathrm{m}}$, triangles), individual-based mating functions, and (b) the mass action mating function ($\mathfrak{B}_{\mathrm{a}}$, diamonds), and the Hölder means mating function ($\mathfrak{B}_{\mathrm{h}}$, dots). Parameters: $\tau = 20$ (individual-based); $c\tau = 1$ (mass action); $\alpha = -\infty, \beta = 0.5$ (Hölder); with $b = 1$, $r = 0.2$, $v_{\mathrm{m}}+v_{\mathrm{f}} = 2$ and $\mu = \phi = 4$.

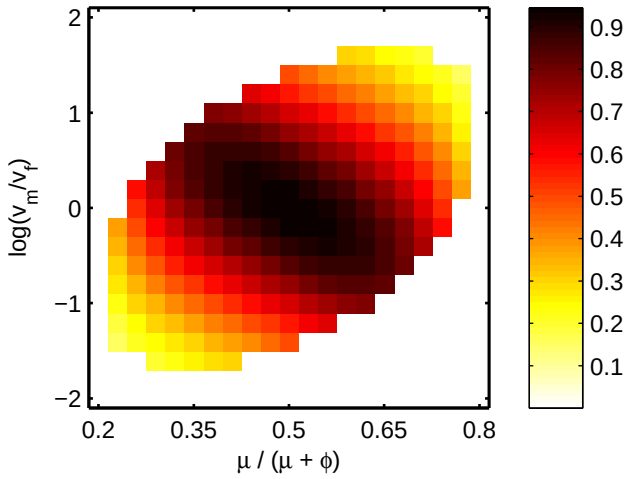

Figure 15: The long-term invasion speed (averaged across generations 90 to 100) as a function of the skew in sex ratio (x-axis) and the degree of sex bias in dispersal (y-axis), calculated from simulations with the unbiased individual-based mating function, $\mathfrak{B}_{\mathrm{u}}$. Parameters: $\tau = 20$, $b = 1$, $r = 0.2$, $v_{\mathrm{m}} + v_{\mathrm{f}} = 2$ and $\mu + \phi = 8$.

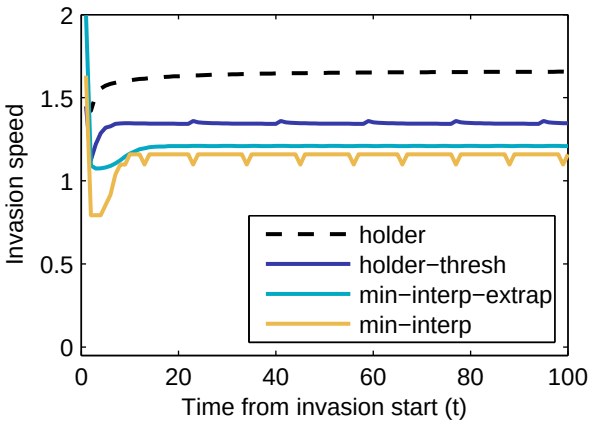

Figure 16: The invasion speed over time for simulations with different levels of interpolation/extrapolation.